# Aspects of adaptive radiation in Southern African Accipiters

by

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## ABSTRACT

Some aspects of the adaptive radiation of African accipitrine hawks are discussed in this study, based on the wing and culmen measurements of seven species; *Accipiter minullus* (Daudin), *A. badius* (Gmelin), *A. ovampensis* (Gurney), *A. rufiventris* (Smith), *A. tachiro* (Daudin) and *A. melanoleucus* (Smith), and *Melierax gabar* (Daudin). These measurements are discussed in relation to observations on habitats and hunting methods. The species were found to be spread over an even size-gradient, though they form three groups in size, habitat and hunting methods. In all seven species the female is larger than the male. *A. ovampensis* and *A. rufiventris* are morphologically similar but appear to be allopatric. *M. gabar* appears to have occupied an available position in the Accipiter series.

## INTRODUCTION

There has been little work on the adaptive radiation of African accipitrine hawks. Recent work on the three North American species of *Accipiter* show size differences between the sexes and species forming a size-gradient. The males are smaller than the females and tend to take smaller prey (Storer, 1966). The situation in the African sub-continent has not yet been studied with respect to size-gradient, inter- and intra-specific competition and habitat preferences.

This study is based on the wing and culmen measurements of seven species: *Accipiter minullus* (Daudin), *A. badius* (Gmelin), *A. ovampensis* (Gurney), *A. rufiventris* (Smith), *A. tachiro* (Daudin), *A. melanoleucus* (Smith) and *Melierax gabar* (Daudin), supported by observations of habitat and hunting methods of each species both in the field and in captive specimens. *Melierax gabar* was included in the study owing to its similar appearance and habits. These measurements are then interpreted in terms of the adaptive radiation of the two genera.

## METHODS AND MATERIAL

Measurements were taken of adult specimens in the collection housed in the National Museum, Bulawayo, Rhodesia. Though the number of specimens could have been increased by the addition of immature birds, it was found that the proportion of mis-sexed birds was high, while some specimens had obviously not reached full size. The high proportion of mis-sexed birds probably resulted from the mis-identification of the paired ovaries (usual in these genera) for testes. A few adult specimens were also mis-sexed and were either re-sexed correctly or omitted. The specimens used in this study were:

| | | |
|---|---|---|
| *A. minullus* | 15 ♂♂ | 8 ♀♀; |
| *A. badius* | 20 ♂♂, | 38 ♀♀; |
| *A. ovampensis* | 5 ♂♂, | 6 ♀♀; |
| *A. rufiventris* | 2 ♂♂, | 4 ♀♀; |
| *A. tachiro* | 10 ♂♂, | 7 ♀♀; |
| *A. melanoleucus* | 3 ♂♂, | 1 ♀♀; |
| *M. gabar* | 26 ♂♂, | 29 ♀♀. |

Wing and culmen measurements were chosen as two features best reflecting adaptation to hunting. Though body length could have been used, it was found that specimens differed considerably as a result of skin preparation. The wing measurements were taken from the wrist to the tip of the longest primary when pressed flat on a metre rule, while the culmen was measured with calipers from the tip to the naso-frontal suture at the base of the culmen.

The means and standard deviations of these measurements were calculated (Table I) and a plot of wing length against culmen length is shown in Figure I, in which the range of each measurement is represented by the standard deviation. The regression lines for wing/culmen length (1) and culmen/wing (2) were calculated by the method of least squares (Simpson and Roe, 1939).

TABLE I. Wing and culmen measurements of six *Accipiter* spp. and *Melierax gabar*

| Species | ♂♂ | | | | | ♀♀ | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | No. of Specimens | Culmen | | Wing | | No. of Specimens | Culmen | | Wing | |
| | | Mean | St. Dev. | Mean | St. Dev. | | Mean | St. Dev. | Mean | St. Dev. |
| *A. minullus* | 15 | 15·2 | 0·37 | 141 | 3·8 | 8 | 16·9 | 0·39 | 162 | 4·3 |
| *A. badius* | 20 | 16·6 | 0·60 | 176 | 4·4 | 38 | 18·1 | 0·74 | 195 | 4·8 |
| *A. ovampensis* | 5 | 18·4 | 0·48 | 221 | 5·2 | 6 | 22·0 | 0·92 | 248 | 6·3 |
| *A. rufiventris* | 2 | 18·7 | 0·99 | 219 | 1·4 | 4 | 21·9 | 1·06 | 240 | 3·9 |
| *A. tachiro* | 10 | 23·5 | 0·77 | 215 | 6·9 | 7 | 27·9 | 1·56 | 251 | 5·2 |
| *A. melanoleucus* | 2 | 28·3 | 1·40 | 295 | 10·7 | 1 | 32·8 | — | 329 | — |
| *M. gabar* | 26 | 18·4 | 0·48 | 186 | 4·1 | 29 | 20·7 | 0·67 | 200 | 6·3 |

## HABITATS AND HUNTING METHODS

The separation of the species in Figure 1 into relatively shorter or longer winged forms suggested a relationship between wing length, habitat preference and hunting methods. However, as a review of the literature on the African Accipiters showed considerable confusion as to the habitat preferences and hunting methods of these hawks, it was felt that a fuller discussion of these aspects was necessary for the purposes of this study.

All the accipitrine hawks make use of several well-known hunting methods, and the extent to which each is used varies with the species. The most acceptable terminology for these different methods is that used by falconers, and these are used here as the most descriptive terms available.

The Accipiters "prospect" for concentrations of prey by flying high over the area at no great speed; the characteristic pattern is a succession of glides interrupted by a series of fast wing-beats. The prospect flight is particularly well-known in the African Goshawk *A. tachiro*. Their success in hunting, however, depends on more secretive or surprise tactics. Quiet waiting or "still-hunting" on an exposed branch, or behind screening foliage for suitable prey, followed by a swift plunge through the trees, with wings partially folded, is a method most suited to heavily wooded areas (Grossman and Hamlet, 1964).

A second, more active, method of hunting is known as "speculative hunting" which is distinct from the prospect flight. The bird flies at considerable speed a few feet above the ground in open areas, or just below tree-top level in wooded areas, taking advantage of any irregularities of terrain. A low glide is followed by a lightning swerve over the top of any likely thicket to surprise any prey on the other side. This opportunistic method had been described for *A. nisus* in Europe by Mavrogordato (1960) and for *A. gentilis* in North America by Beebe (1964).

These methods may be considered typical of the Accipiters. Some species clearly prefer one method, while others are sufficiently adaptable to use both methods with equal success. Beebe states that of the three North American species, *A. velox* is the most aerial, and does less still-hunting than either *A. gentilis* or *A. cooperi*. He states further that it shows a definite preference for open or sparsely-treed country rather than thick woods.

*A. minullus*

This species inhabits continuous or riverine forest where the cover is thick enough for still-hunting to be used to the full. A hawk this size is able to find cover even in relatively thin forest, and this secretive hunting habit is suggested as the reason for its apparent scarcity in areas where it may well be common. The captive bird, once tamed, "bates" (flying off the hand, often through restlessness) less frequently than any other Accipiter except *A. tachiro*, which may be considered the most relaxed of the African bird hawks.

*A. badius*

The Little Banded Goshawk occupies a similar habitat to *A. minullus*, but it appears to prefer more open woodland, and the range of habitats is less broad. While *A. minullus* is a fairly common breeding resident of the eastern Cape coastal belt, *A. badius* has only rarely been recorded on the fringe of this region, in dry, open country (Paterson, 1958). In captivity, this is a more restless hawk than either *A. minullus* or *A. tachiro*. It is a fairly fast flier, though not strongly orientated to bird prey, and much of its diet may consist of insects and small reptiles.

*A. ovampensis*

This species inhabits the open savannah veld (open woodland) and is also common in almost treeless grassland such as certain areas of the Transvaal highveld. In a similar way to *A. rufiventris*, it may often be found nesting in a small grove of trees in an otherwise treeless area (Black, personal observations). In captivity, it has been found to be a very swift flier, strongly orientated to bird prey. It is a restless, fierce hawk, not disdaining to chase the most swift of quarry such as quail (Savory, personal communication). In most areas inhabited by *A. ovampensis* there is little opportunity to use the method of still-hunting, and this species is almost entirely a speculative hunter.

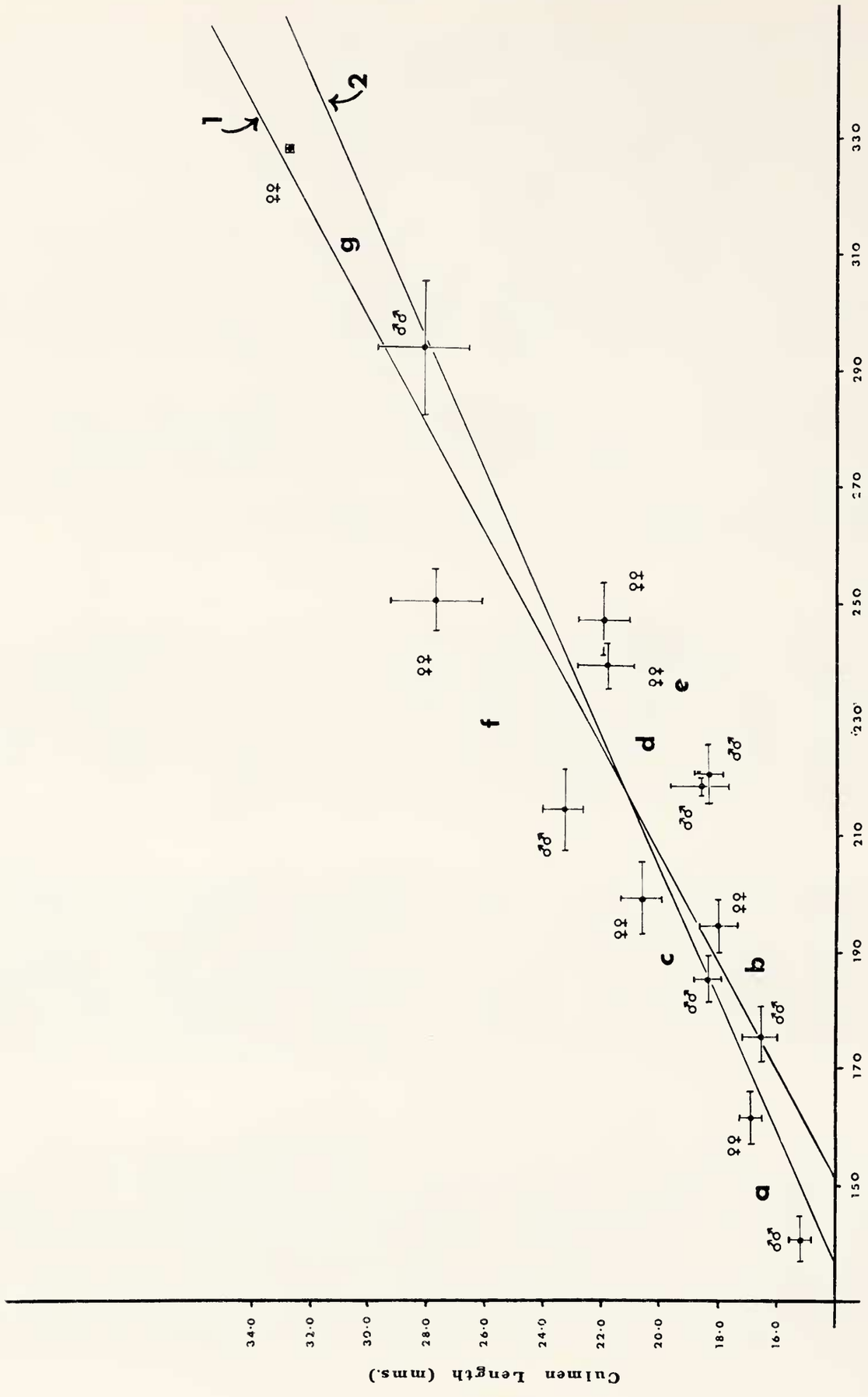


Fig. 1. A plot of the means and standard deviations of the wing and culmen lengths in the seven species: a = *A. minullus*; b = *A. badius*; c = *M. gabar*; d = *A. rufiventris*; e = *A. ovampensis*; f = *A. tachiro*; g = *A. melanoleucus*.
(Line 1 = regression of wing length/culmen length)
(Line 2 = regression of culmen length/wing length)

*A. rufiventris*

Contrary to the majority of literature on *A. rufiventris* this hawk is not strictly a forest form, and observations have shown that it spends a good deal of time on the move, and is almost invariably seen on the fringe of, or in open country. It is common in certain areas of the Karoo, such as Graaff-Reinet (Black, personal observations), where it breeds in a few acres of poplars separated from the next grove by several miles, in otherwise treeless country. Its occurrence in the eastern highlands of Rhodesia (Rushworth, personal communication) and in Basutoland (Jacot-Guillarmod, 1963), where the wooded areas are separated by large tracts of open country, also show its preference for less wooded country. The distribution, hunting habits and size suggests that it is the ecological replacement of *A. ovampensis* in mountainous regions and to the south of the latter's range. Observations on the trained bird indicate that it relies on speculative rather than still-hunting and is strongly orientated to bird prey; this is further reflected in its restlessness in captivity.

*A. tachiro*

Dense forest and thick riverine forest form the optimum for this species, which becomes increasingly scarce as the cover thins out towards the west. It is a very secretive hawk, relying on still-hunting more than any other *Accipiter* sp. (Black, 1968). Its great disadvantage from the falconer's point of view is its habit of attacking only when it senses an overwhelming advantage over the prey. It shuns a long, hard chase, and immediately recognizes certain slow-flying species such as loeries and coucals.

*A. melanoleucus*

This species appears to be equally common in open woodland as in thick forest. It is an extremely fast and relentless bird in the chase, and has been seen chasing homing pigeons for long distances. In general hunting habits, it uses both speculative and still-hunting with equal success.

*Melierax gabar*

The Gabar Goshawk is absent from the dense coastal forest, but inhabits a wide variety of habitats ranging from dry woodland through lightly wooded savannah into the more arid areas of South-West Africa, where there is suitable cover (dense riverine scrub). The captive bird is fast and relentless, and is strongly orientated to bird prey, although less so than *A. rufiventris* or *A. ovampensis*. Observations in the field indicate that it uses a modified form of still-hunting. It is often found waiting on an exposed branch for its prey, but the attack may well include a fairly long chase.

## DISCUSSION

Figure 1 shows two points clearly; the female of all seven species is always larger than the male, with no overlap, and the species are spread over an even size-gradient.

While it is agreed by Amadon (1959), Cade (1960) and Selander (1966) that the "reversed" sexual dimorphism of raptors is correlated with predatory habits, there is some disagreement as to the origin of this dimorphism. Amadon and Cade suggest that the larger size of the female is related to the difficulty of pair formation in predatory birds, while Selander suggests "the basic adaptive function of the dimorphism is related to differential niche utilization".

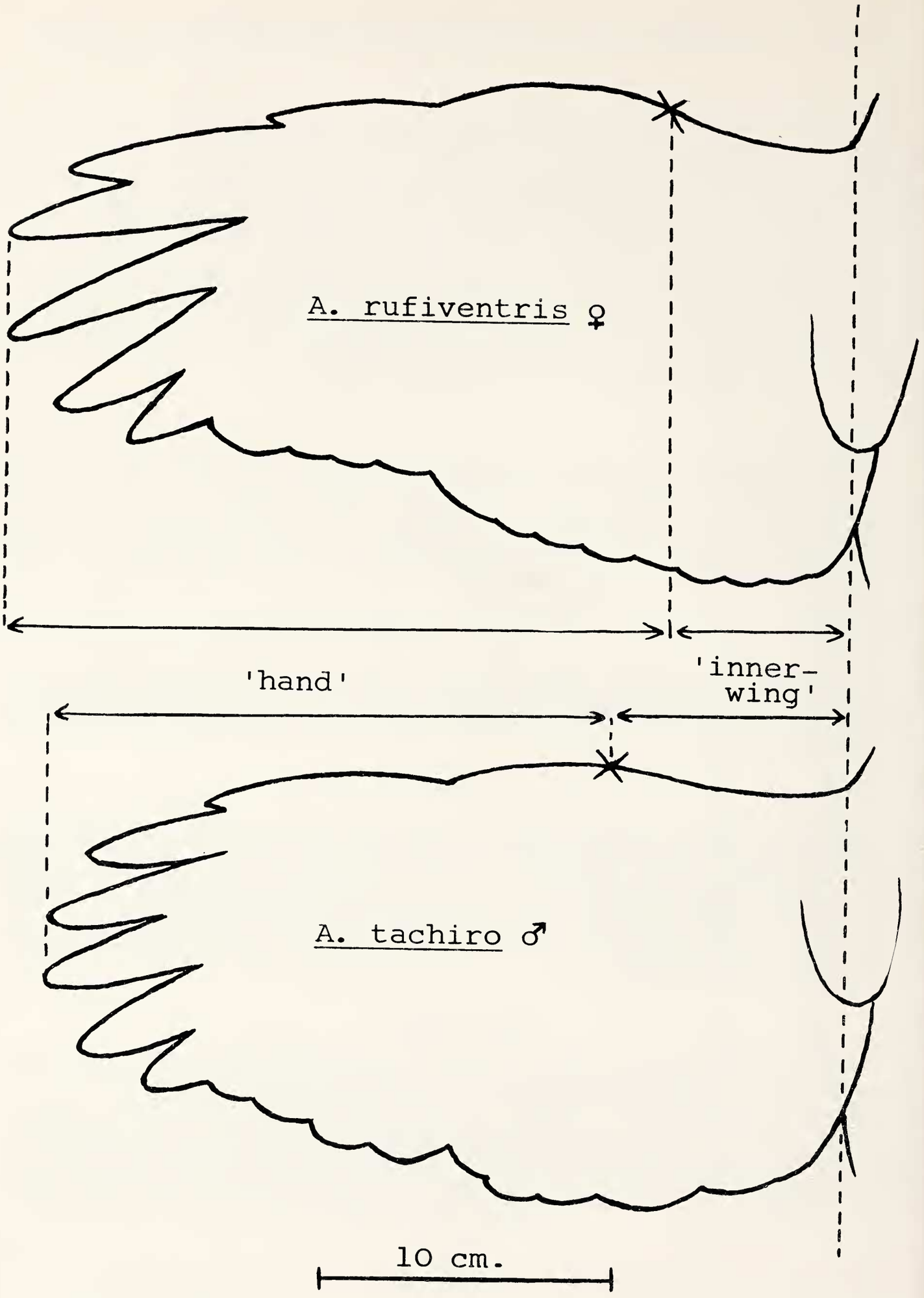


Fig. 2. The outlines of the wings of juvenile ♀ *A. rufiventris* and ♂ *A. tachiro*, illustrating differences in the proportions of the wing.

Storer (1966) has shown that the males do take smaller prey in three North American *Accipiter* spp. and it is assumed that the same holds true for the African species discussed here.

Storer has also shown that the size of prey is directly related to the size of the hawk; this reduces inter-specific competition to a minimum, and results in an even exploitation of the available prey (cf., Crombie, 1947). The American *Accipiter* spp. however, are sufficiently separated in size to allow a considerable overlap in habitat.

There is a considerable overlap in size in the African species, as is shown in Figure 1. However, it is found that the species fall into three groups separated by the regression lines 1 and 2, and that these groupings can be related to habitat preferences and hunting methods.

Those species with a shorter wing relative to beak length, appearing above the regression line 1, are *A. minullus*, *A. tachiro* and *M. gabar*. These are all species preferring dense cover, and using still-hunting predominantly. *M. gabar*, however, tends to be less separated than either *A. minullus* or *A. tachiro*, as reflected in both Figure 1 and in its habitat and hunting methods. The second group, appearing below the regression line 2, is composed of *A. badius*, *A. rufiventris* and *A. ovampensis*, whose wings are longer relative to beak length. These are all species inhabiting more open country, and in which speculative hunting predominates. In fact, *A. rufiventris* and *A. ovampensis* are the longest winged and most aerial of all the African *Accipiter* spp. The third group, containing *A. melanoleucus*, lies between the regression lines 1 and 2, and its intermediate position relates well to its habitat preferences and intermediate hunting habits. The speed of this species is a reflection of its size rather than its wing length, for the larger a bird, the faster it must fly to stay airborne (Storer, 1966).

At first, these groupings suggest that a shorter wing has some advantage in dense cover, such as aiding in manoeuvrability. At this point, however, it is important to remember that the wing length referred to in the proceeding discussion is that from the wrist to the tip of the wing (hand) only, and not of the whole wing. The primaries provide the propulsive force in flight, while the inner part of the wing acts as a relatively stationary aerofoil, providing lift. Thus a fast-flying bird requires a larger area of wing for propulsion, and a correspondingly smaller area for lift than a slower flier, e.g., swifts (Harrison, 1964).

Figure 2 shows the wing patterns of perhaps the most extreme examples of this effect in the African *Accipiter* series, taken from two specimens soon after death. Figure 2a is the wing of a juvenile ♂ *A. tachiro* weighing 205 gm. ($7\frac{1}{4}$ oz.) while Figure 2b shows that of a juvenile ♀ *A. rufiventris* weighing 220 gm. ($7\frac{3}{4}$ oz.). While these two birds are of comparable weight and size, and the wings are almost identical in length, the proportions of the hand length and the forearm length differ considerably. The greater length of the forearm in *A. tachiro* is clearly an adaptation providing lift and manoeuvrability while flying relatively slowly in dense cover. Similarly the longer hand of *A. rufiventris* is an adaptation to fast flight.

An experiment by Chapeau on the flight of doves emphasizes the importance of the primaries in the propulsion of the bird. The removal of a small portion of the tips of the primaries prevented a dove from flying, while the reduction of 55% of the total wing area by removing secondaries still permitted flight (Welty, 1962). This is an indication of the importance of the differences in the hand length of these *Accipiter* spp.

A further important factor as yet undiscussed is the breadth of the wing, in particular in the region of the forearm, where the breadth is the same as the length of the secondaries. This length and that of the forearm determine the wing area of the inner part of the wing and thus the lifting capacity of the wing. The preparation of specimens precluded the measurement of wing breadth and area, but some indication of these can be seen in Figure 3, where each species has been traced from photographs. The length of primaries showing beyond the secondaries when the wing is folded back varies from species to species. This length reflects the proportion between the length of the hand to the length of the secondaries and to a lesser extent that of the forearm as well, as is shown in the partially open wing of *A. ovampensis*

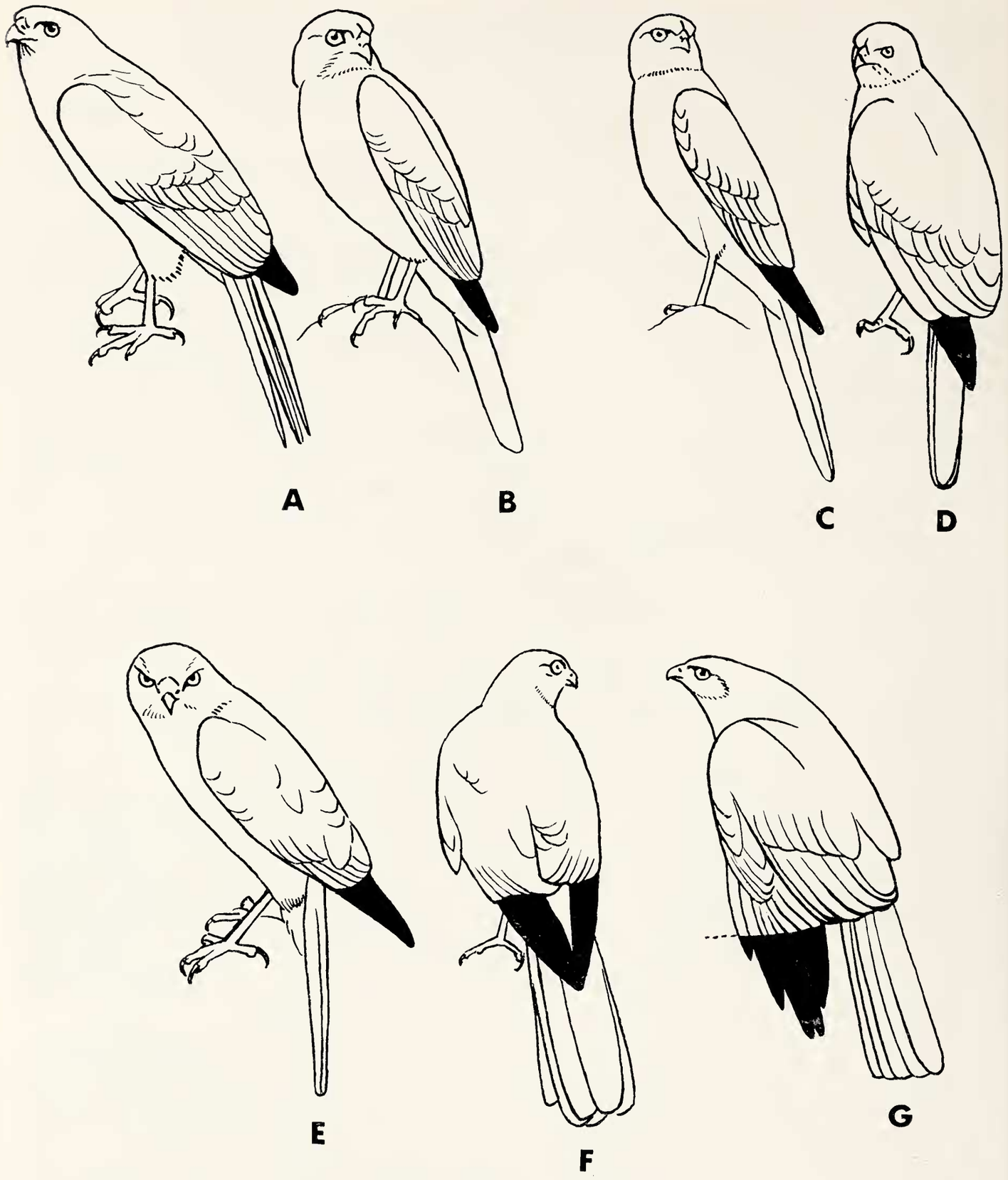


Fig. 3. Outline tracings from photographs illustrating the estimation of inner-wing area from the length of primaries extending beyond the secondaries (shaded black): A = *A. tachiro*; B = *A. minullus*; C = *M. gabar*; D = *A. melanoleucus*; E = *A. badius*; F = *A. rufiventris*; G = *A. ovampensis*

in Figure 3g. It is interesting to note that those species demonstrated on this basis to have the largest inner-wing area are the dense cover species *A. tachiro*, *A. minullus* and *M. gabar*, while those with the smaller area are *A. rufiventris and A. ovampensis.*

The almost complete overlap in size and proportions of *A. rufiventris* and *A. ovampensis* indicates competition for the same prey. The two species may be considered allopatric, for their ranges only overlap slightly in the eastern highlands of Rhodesia and north-eastern Transvaal, where *A. ovampensis* is reported to be sparse (Rushworth, personal communication).

Judging from the numbers of species of the range of the genus *Accipiter*, it may well be considered the most successful of the sub-family Accipitrinae. It is generally considered that the genus *Melierax* is an offshoot within the main stem of the group. Of the three species *M. musicus* and *M. metabates* are extremely successful in their own niches; they are *Buteo*-like in habits, with relatively little resemblance to the typical bird-hawks. *M. gabar*, however, differs considerably in habits and habitat from *M. musicus* and *M. metabates.* Its position in Figure 1 suggests that it has adapted as a typical bird hawk, filling an available gap in the *Accipiter* series.

## ACKNOWLEDGEMENTS

The authors wish to thank Mr M. P. S. Irwin for the use of specimens, and for much help during the initial part of the study. We also wish to thank D. Rushworth and A. Savory for their useful comments on distributions and habits.

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